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PATTERNS OF FIRST-YEAR GROWTH IN POPULATIONS OF DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* VAR. *GLAUCA*)

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ABSTRACT

One-year-old seedlings representing 56 populations of Douglas-fir from the Inland Northwest expressed variation in patterns of growth. Population means for the percentage of seedlings with a single period of epicotyl elongation varied from 1 percent to 81 percent. A multiple regression of the percentage of seedlings with one growth period on geographic and ecologic variables of the seed source accounted for 40 percent of the variation in the dependent variable.

KEYWORDS: ecological genetics; Rocky Mountain Douglas-fir; seed zoning; geographical variation; growth patterns.

Seed zones are based on variation in numerous traits that reflect adaptation to the natural environment. For Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in the Northern Rocky Mountains, variation in growth, phenology, and freezing tolerance reflects adaptations to three relatively distinct environmental provinces: (1) northern Idaho and northeastern Washington, (2) western Montana, and (3) relatively cool environments regardless of geography (Rehfeldt 1978).

Current research is assessing adaptation of populations within the northern Idaho province, which is bounded by the Columbia River in northeastern Washington, the Salmon River in northern Idaho, and the state line between Idaho and Montana. Within this province populations of greatest cold hardiness in early autumn tend to be from high latitudes, high elevations, and subalpine habitat types (Rehfeldt in press).

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The present study was begun to determine if populations of Douglas-fir differ in their ability to tolerate drought, and to incorporate variation in drought resistance into seed zones for northern Idaho. One-year-old seedlings were exposed to moisture stresses by withholding water. However, all variation among populations in ability to endure the imposed stress was explained by the proportion of seedlings from each population that had either one or two periods of shoot elongation. But since the end of the first period of elongation or the beginning of the second period occurred before seedlings were subjected to the moisture stress, the data only reflected variation in the pattern of first-year growth.

METHODS

Patterns of growth were observed in 1-year-old seedlings representing 56 populations from the Inland Northwest (fig. 1). Most of these populations were from the northern Idaho environmental province, but populations from the following peripheral areas were also included: northeastern Oregon, north central Washington, central Idaho, and Montana east of the Cabinet Divide.

Populations from the northern Idaho province were selected from the five habitat types (Daubenmire and Daubenmire 1968) on which Douglas-fir is most common. However, few populations were selected from the *Abies lasiocarpa* series of habitats; adaptive differentiation has already been associated with the cool environments of these habitat types (Rehfeldt 1978). In addition, an attempt was made to reduce confounding among the latitudes, longitudes, elevations, and habitat types represented by populations from northern Idaho. Interrelationships among these variables are expressed in the following matrix of correlation coefficients:

	Interclass Correlations		*Intraclass correlations*
Variable	*Longitude*	*Elevation*	*Habitat type*
Latitude	0.67**	-0.22	0.12
Longitude		-.35*	.01
Elevation			.23*

*Statistical significance at the 0.05 level of probability.
**Statistical significance at the 0.01 level of probability.

The strong correlation between the latitude and longitude of population origin reflects the physical shape of northern Idaho (fig. 1). Habitat types accounted for 23 percent of the variance in elevation of the populations reflecting a general altitudinal distribution of habitat types (Daubenmire and Daubenmire 1968).

For each of two replications of a randomized complete block design, 21 seedlings from each population were grown in plastic containers (150 cm^3). Seeds were sown in early May, and seedlings were grown in a greenhouse under natural day length and optimal levels of moisture until late June, when the containers were watered until soil moisture reached saturation. No additional water was added for the remainder of the study. Greenhouse temperatures ranged from 27° to 38°C during the day and from 10° to 16°C during the night. For each seedling, the date the germinated seed emerged was recorded and the number of periods (1 or 2) of epicotyl elongation scored.

In order to assess adaptive differentiation of populations, an analysis of variance was made on the proportion of seedlings that exhibited a single period of growth. Multiple regression analyses were made to relate mean performance of populations to geographic and ecologic criteria of the seed source. The following model was used:

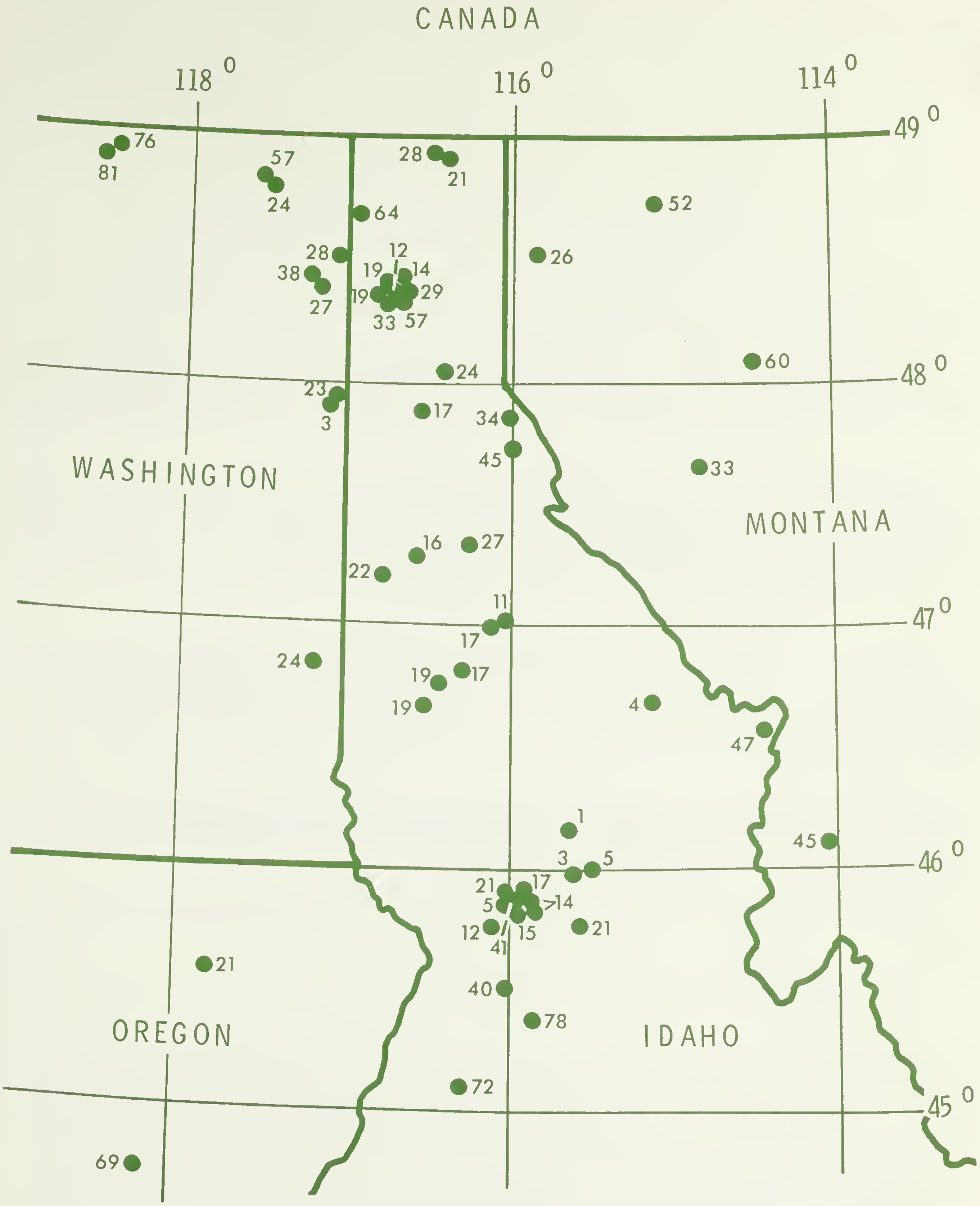

FIGURE CAPTION

Figure 1.--Location of populations (dots) and mean percentage (numbers) of seedlings with a single period of first-year elongation.

$$Y_i = b_0 + b_1 X_{i1} + \ldots b_7 X_{i7}$$

where:

Y_i = proportion of seedlings from population i that had one period of growth.

X_{i1} = degrees latitude at the origin of population i.

X_{i2} = degrees longitude at the origin of population i.

X_{i3} = meters ($\times 10^{-2}$) elevation at the origin of population i.

X_{i4} to X_{i7} = constant terms that respectively code the *Pseudotsuga menziesii*, *Abies grandis*, *Thuja occidentalis*, and *Tsuga heterophylla* habitat types.

Under this model, effects of the *Abies lasiocarpa* habitat types are included in the intercept (b_0), which also includes the general mean. Regression coefficients for constant terms are deviations from b_0 that reflect effects of particular habitat types.

RESULTS AND DISCUSSION

Near the end of June, 1-1/2 months after seeds were sown, seedlings began to form terminal buds. Only 71 percent of the seedlings resumed growth. Since containers were last watered near the end of the first period of elongation, the pattern of growth was not influenced by moisture stress. Mortality from moisture stress did not begin until mid-August, 1-1/2 months after the final watering.

Seedlings with only a single period of epicotyl elongation averaged 15 mm shorter than those with two periods, even though the growing season was curtailed by moisture stress; moreover, the pattern of growth did not seem to be related to the date of emergence. Although emergence took place over an interval of 15 days, the mean day of emergence for seedlings with one or two periods of growth was 17.6 and 18.2 days after sowing, respectively.

Individual populations were characterized by as little as 1 percent and as much as 81 percent seedlings that had only one period of shoot elongation (fig. 1). That mean differences are real is suggested by the following analysis of variance:

Source of variation	*df*	*Intraclass correlation*	*Level of significance of F-value*
Replications	1	0.02	5%
Populations	55	.77	1%
Rep. x Pop.	55	.21	--

Since the primary objective of the study was to assess adaptive differentiation of populations from the environmental province that includes northern Idaho and eastern Washington, populations from peripheral areas were excluded from multiple regression analyses. Peripheral populations likely represent contrasting environmental provinces (Wright and others 1971; Rehfeldt 1978) for which multivariate relationships differ from those of the northern Idaho province.

The multiple regression analysis was significant at the 1 percent level of probability and accounted for 40 percent of the variation in the dependent variable. Differences between observed values and those predicted by the regression model were examined to ensure that error variances were homogeneous and that there was no visual evidence of lack of fit of data to the equation. Standarized partial regression coefficients (b') for the independent variables are:

	Variable	*b'*
Y_1	latitude	0.32
Y_2	longitude	.17
Y_3	elevation	.29
	habitat type:	
Y_4	*Pseudotsuga menziesii*	-.20
Y_5	*Abies grandis*	-.21
Y_6	*Thuja occidentalis*	-.23
Y_7	*Tsuga heterophylla*	.18

Standardized partial regression coefficients, which depict the relative influence of the independent variables in determining the dependent variable, indicate that latitude and elevation are major determinants of pattern of first-year growth in populations from north Idaho. Latitude and elevation are related to the dependent variable by statistically significant (1 percent level) simple correlation coefficients of 0.47 and 0.43, respectively.

In addition, the regression statistics also suggest that habitat types were influential. In fact, habitat types alone accounted for 23 percent of the variation among populations; and the associated F-value was significant at the 5 percent level of probability. Mean values for Idaho populations from the five habitat types were:

Habitat series	*Number of populations*	*Percentage seedlings with one growth period*
Pseudotsuga menziesii	10	20.7
Abies grandis	12	19.4
Thuja occidentalis	14	21.1
Tsuga heterophylla	5	35.5
Abies lasiocarpa	4	40.9

Since regression coefficients for constant terms reflect mean values, tests for differences among coefficients for the various habitat types are essentially tests for differences among the mean values listed above. Tests of "*t*" for differences in regression coefficients implied that the two greatest mean values differed significantly from the three lowest; however, previous results (Rehfeldt 1978; in press) make it doubtful that populations from the *Tsuga* habitat types are more similar genetically to populations from cold environments than to those from similar mesic environs. One of the five populations from a *Tsuga* habitat type represented the broad Priest Lake valley in northern Idaho. Much of the vegetation in this valley represents an ecotone between the *Tsuga* and *Abies lasiocarpa* series. This particular population was characterized by an unusually high proportion (64 percent) of seedlings with only one growth period. If this population is included in the subalpine series of habitat types, no differences can be detected among the *Pseudotsuga*, *Abies grandis*, *Thuja*, and *Tsuga* habitat types. Thus, it seems that the effects of habitat types in the regression analysis result primarily from the performance of seedlings from *Abies lasiocarpa* habitat types, which contrasts with that of seedlings from the other habitat types.

Multiple regression analyses account for average performance in relation to geographic and ecologic factors. Still, the performance of several individual populations should be mentioned. Populations from *Abies lasiocarpa* habitat types from two small frost pockets at 820 m and 950 m elevation did not express similar patterns of elongation and rates of cold acclimation (Rehfeldt 1978; in press) to populations from subalpine environments at relatively high elevations. Yet, seedlings representing a population from a large frost pocket in the Priest Lake valley, elevation 900 m, performed similarly to those from high elevations. Evidently, the genetic composition of trees occupying a frost pocket depends on the size of the pocket and availability of a suitable seed source as well as variation in environmental selection coefficients.

Populations from areas peripheral to the central area of study produced the following proportions of seedlings with one growth period:

Area of origin	*Number of populations*	*Percentage seedlings with one growth period*
Blue mountains, northeastern Oregon	2	43
Okanogan Mountains, northern Washington	2	78
Montana east of the Cabinet Divide	4	47
Central Idaho	3	63

Even when the elevation and habitat type of population origin are considered, populations from the peripheral areas were characterized by a much higher proportion of seedlings with only one growth period than populations from northern Idaho and northeastern Washington (fig. 1). As suggested previously (Wright and others 1971; Rehfeldt 1978), these peripheral populations likely represent environmental provinces of adaptational norms different from those of northern Idaho and eastern Washington.

Irgens-Moller (1968) and Sorensen[2] have also observed variation in patterns of growth in Rocky Mountain Douglas-fir. Consequently, variation among populations in patterns of growth does not seem to be an artifact induced by cultural conditions. Positive relationships were observed between the latitude or elevation of the seed source and the proportion of seedlings with a single period of growth. These results are similar to those involving variation in cold hardiness of Douglas-fir populations (Rehfeldt in press). In fact, 38 of the populations represented in the present study were also included in freezing tests for hardiness. That the pattern of growth is related to autumnal dormancy and thereby to the length of the growing season is suggested by the statistically significant (1 percent level) simple correlation ($r = 0.57$) relating measures of hardiness in early autumn to the proportion of seedlings that expressed a single growth period.

Because of the correspondence between current and previous results on variation of Douglas-fir populations from northern Idaho, practical implications of current data are similar to those based on variation in cold hardiness: seed zones for northern Idaho and eastern Washington should not encompass more than 1-1/2° latitude and 400 m elevation; and *Abies lasiocarpa* habitat types seem to represent a separate zone (Rehfeldt 1978; in press).

This study represents one of a series on the ecological genetics of Douglas-fir in the Northern Rocky Mountains. It has shown that populations are differentiated according to the pattern of first-year growth. At the present time, little is known about this trait, but if it is related to adaptive differentiation, the genetic and environmental controls of patterns of first-year growth need further study.

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